

A New Cheilostome Bryozoan with Gigantic Zooids from the North-West Pacific

Andrei V. Grischenko^{1*}, Paul D. Taylor² and Shunsuke F. Mawatari¹

¹*Laboratory of Systematics and Evolution, Division of Biological Sciences,
Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan*

²*Department of Palaeontology, The Natural History Museum,
Cromwell Road, London SW7 5BD, UK*

ABSTRACT—*Gontarella gigantea* gen. et sp. nov. is described from two stations, one in the Sea of Okhotsk and the second on the Pacific side of the Small Kuril Arc. This membraniporiform anascan cheilostome bryozoan has very large zooids, the largest known among extant sheet-like encrusting anascans. Comparative data on similar sheet-like cheilostomes gathered from the literature shows that the new species represents a conspicuous outlier in size, with the surface area of the zooid being approximately twice that of the next largest species. Skeletal evidence, including the lack of ovicells, indicates that *G. gigantea* belongs within the malacostegan family Electridae. The gigantic ancestrula suggests that the species has a cyphonautes larva about 1 mm in maximum dimension.

Key words: bryozoans, taxonomy, zooidal size

INTRODUCTION

Body size has long been a focus of interest among biologists. For example, research has sought to record and understand latitudinal gradients in body size, the implications of size for organismal physiology, and the relationships between size and life history strategy. Most studies have dealt with unitary, non-colonial animals; there has been very little research on the more complex modular, colonial organisms where body size is expressed at two hierarchical levels: the colony and the zooid. Intraspecific variations in colony size have received some attention (e.g., Grischenko *et al.*, 1999; Barnes and Whittington, 1999). Interspecific variation in bryozoan colony size covers more than three orders of magnitude, the smallest colonies being about 1 mm (e.g., Cook, 1981) and the largest over 1 metre in diameter (e.g., Cocito *et al.*, 1998). Most of this variance is accounted for by differences in the number of zooids in the colony, and not by differences in the size of these zooids. Zooid size, as measured by length and width on the surface of the colony, is relatively uniform within the phylum, especially among marine species.

Temperature-related, intraspecific variation in zooid size among cheilostome bryozoans, the most diverse group of living bryozoans, has attracted recent interest (O'Dea and

Okamura, 1999), as has the genetic vs environmental components of size variation within species (Hageman *et al.*, 1999). However, zooid size variation between species has been relatively neglected, although comparative lophophore size in marine bryozoan populations has been studied (e.g., Ryland, 1975), while McKinney and Jackson (1989) noted correlations between zooid length and colony growth-form. The bryozoan colony growth-form containing the greatest number of species consists of a sheet-like encrustation sometimes referred to as 'membraniporiform'. Zooid length and width in membraniporiform cheilostomes are typically less than 1 and 0.5 mm respectively. Here we describe a new cheilostome genus and species with gigantic zooids up to 1.85 mm long and 1.20 mm wide. Data from the literature on similar sheet-like cheilostomes demonstrates that the new species forms a striking outlier in size – the surface area of zooids in the new species is approximately twice those of zooids in the next largest species.

MATERIALS AND METHODS

Most of the material was collected by AVG in September 1992 during a short cruise on the Middle Fishery Refrigerator Trawler *Rodino* in the Western Kamchatka shelf of the Sea of Okhotsk. Additional material was collected by the Pacific Institute of Bio-Organic Chemistry during the 14th Expedition of the RV *Akademic Oparin*, in September 1991, in north-west Pacific coastal waters of the Habomai Islands (Small Kuril Arc).

Colonies were cleaned in sodium hypochlorite solution, rinsed

* Corresponding author: Tel. +81-11-706-3524;
FAX. +81-11-746-0862.
E-mail: gat@bio.sci.hokudai.ac.jp

with tap-water and dried in air prior to their measurement under a binocular microscope (Nikon SNZ-10). Some dried colonies were coated with Pd-Pt by an ion sputter (Hitachi E-1030) and observed under a scanning electron microscope (Hitachi S-2380N) at 10–20 kV accelerating voltage. Other coated specimens were studied for skeletal ultrastructure using an Hitachi S-2500, and uncoated material, both bleached and unbleached, was examined at low magnifications with an ISI ABT-55 equipped with an environmental chamber and back-scattered electron imager. Mineralogical analysis was performed using an X-ray diffractometer with curved position sensitive detector of 120 degrees arc (Enraf Nonius CPS120).

The specimens described here are deposited in the Zoological Institute, Russian Academy of Sciences (ZIRAS), Saint Petersburg, Russia; Department of Zoology, The Natural History Museum (NHM), London, UK; the Zoological Institute, Faculty of Science, Hokkaido University (ZIHU), Sapporo, Japan; and the National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand.

RESULTS

Systematics

Order **Cheilostomata** Busk, 1852

Suborder **Malacostega** Levinsen, 1902

Superfamily **Membraniporoidea** Busk, 1852

Family **Electridae** Stach, 1937

Genus **Gontarella** gen. nov.

Diagnosis: Colony encrusting. Zooids monomorphic, very

large in size, irregularly rhombic to oval in shape; opesia longitudinally ovoidal, extensive, occupying most of frontal area; gymnocyst lacking; cryptocyst a narrow unornamented shelf, widest proximally, tapering distally, depressed; mural rim irregularly beaded, forming raised zooidal boundary, some zooids having a distal gap in mural rim; basal wall incompletely calcified, containing an oval uncalcified window; pore chambers lacking; vertical walls exterior (i.e. containing a cuticular layer); lateral walls usually with four septulae having an iris-like structure; distal wall with numerous, irregularly arranged rosette plates, some uniporous, others containing up to four pores. Ancestrula single, large, oval; opesia occupying nearly all frontal area; gymnocyst lacking; cryptocyst limited to very narrow proximal shelf; mural rim with sparse, irregular tubercles; pore chambers absent; vertical walls containing numerous pores, 14–16 present in proximal half of zooid, concave, those on left and right sides divided by a narrow median septum; basal wall with oval uncalcified window. Periances-trular buds at least three in number (distal and two disto-lateral), possibly with additional lateral buds forming afterwards; early budded zooids smaller than ancestrula. Skeletal walls calcitic, incorporating a fabric of wedge-shaped granular crystallites.

Table 1. Measurements of zooids of *Gontarella gigantea* gen. et sp. nov. (in mm, except for Nz; all post-ancestrular zooids were measured from the holotype, ZIRAS 1/49944; ancestrulae measured from holotype and NHM 2002.1.7.2)

		Mean	Range	S.D.	Nz
Zooids	L	1.55	1.15–1.85	0.197	30
	W	0.97	0.70–1.20	0.147	30
Opesia	L	1.15	0.92–1.37	0.135	30
	W	0.82	0.57–1.05	0.121	30
Operculum	W	0.39	0.36–0.45	0.028	30
	H	0.24	0.21–0.28	0.025	30
Ancestrula	L	1.07	1.02–1.11	–	2
	W	0.73	0.70–0.75	–	2
Ancestrular opesia	L	0.91	0.87–0.95	–	2
	W	0.63	0.57–0.68	–	2
Ancestrular operculum	W	0.33	–	–	1
	H	0.22	–	–	1

* Abbreviations: L. length; W. width; H. height; Nz. number of zooids; S.D. standard deviation.

Table 2. Astogenetic size variation in *Gontarella gigantea* gen. et sp. nov. (in mm, except for Nz), NHM 2002.1.7.2

Generations	L (zooids)		W (zooids)		L (opesia)		W (opesia)	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
ancestrula	–	1.02	–	0.75	–	0.87	–	0.57
1 (Nz = 3)	0.81–0.87	0.84	0.63–0.69	0.65	0.66–0.69	0.68	0.45–0.54	0.49
2 (Nz = 3)	0.93–1.02	0.97	0.66–0.69	0.67	0.66–0.78	0.74	0.51–0.54	0.52
3 (Nz = 4)	1.08–1.14	1.11	0.69–0.75	0.73	0.75–0.84	0.79	0.54–0.60	0.56
4 (Nz = 5)	1.14–1.23	1.19	0.63–0.75	0.69	0.75–0.90	0.80	0.51–0.54	0.52

* Abbreviations: L. length; W. width; Nz. number of zooids.

Type species: Gontarella gigantea sp. nov.

Etymology. The new genus is named in honour of Dr Valentina I. Gontar (Zoological Institute, Russian Academy of Science, St Petersburg) in recognition of her contributions to bryozoology.

Remarks: This monotypic new genus can be distinguished from existing genera using characters detailed below in the Remarks section of the species description. Principal non-metric characters important in discriminating *Gontarella* from other malacostegan anascans are the lack of gymnocyst and spines, non-granular cryptocyst forming a narrow sunken shelf proximally, absence of pore chambers, ancestrula with numerous septular pores around the perimeter, distal and two distolateral periancestrular buds but no proximal periancestrular bud, periancestrular zooids smaller than the ancestrula, and calcitic skeleton with wedge-like granular ultrastructure.

***Gontarella gigantea* sp. nov.**

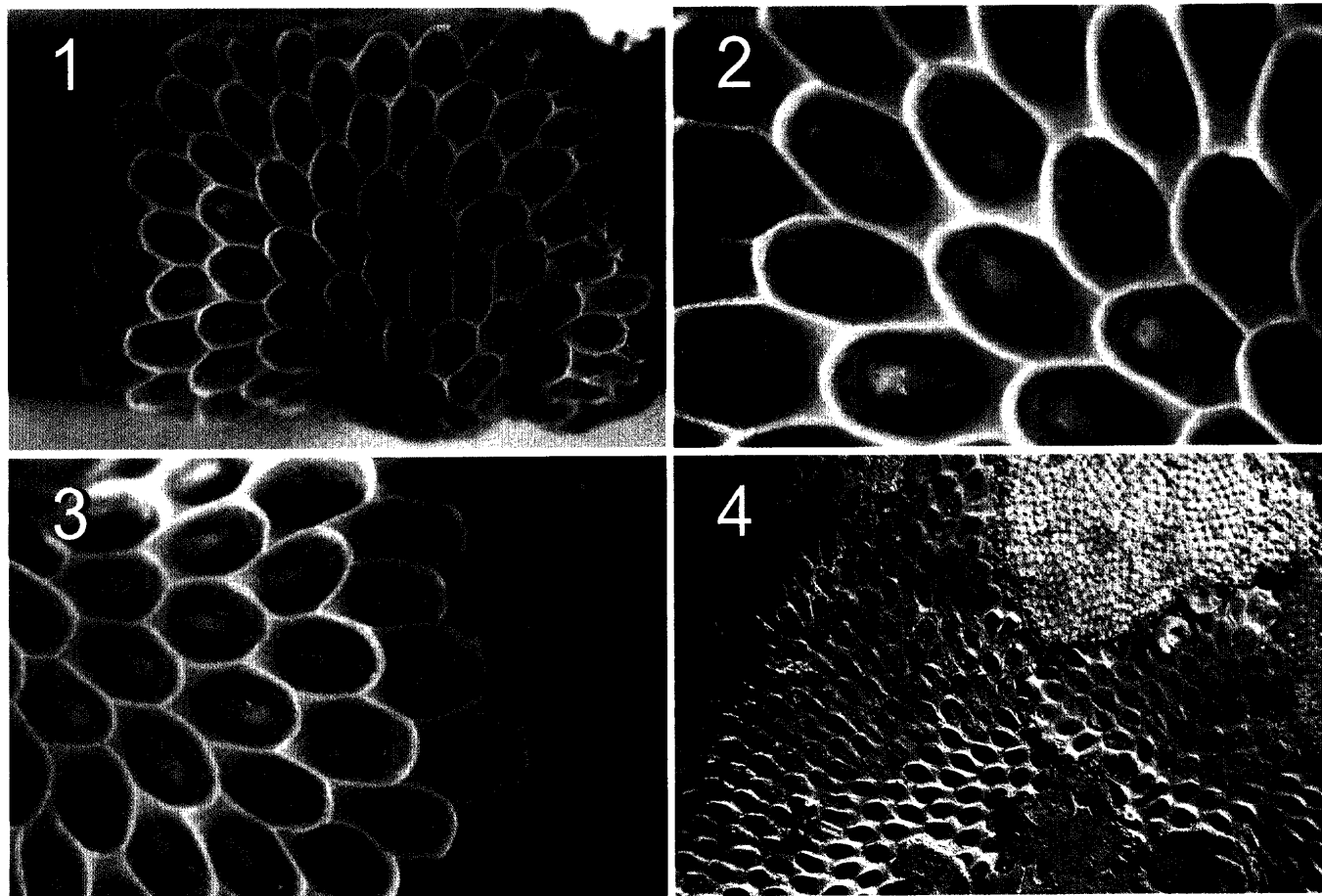
(Figs 1–18)

Material examined: Holotype: ZIRAS 1/49944 (one colony on polychaete tube; preserved in alcohol), Pacific Institute of Bio-Organic Chemistry Collection dredged during the 14th Expedition of the RV *Akademic Oparin*, Stn 94, 10 September 1991, north-west Pacific Ocean in the coastal waters

of the Habomai Islands, Small Kuril Arc (43°10.2'N, 146°18.2'E), depth 535 m, bottom silty sand, Trawl Sigsby, collector A.V. Smirnov. Paratypes: NHM 2002.1.7.1 (large colony on a stone), NHM 2002.1.7.2 (small ancestrulate colony on a stone), ZIHU-02049 (one colony on a stone), ZIHU-02050 (colony fragment detached from hydrocoral *Allopora* sp.), NIWA P-1273 (one colony fragment on a stone); sorted from a crab trap by A.V. Grischenko on the Middle Fishery Refrigerator Trawler *Rodino*, 12 September 1992, Western Kamchatka Shelf of the Sea of Okhotsk, about 32 km from Cape Hayryuzova (57°36.2'N, 156°09.0'E), depth 78–81 m, bottom silt, sand and gravel.

Measurements: See Tables 1 and 2.

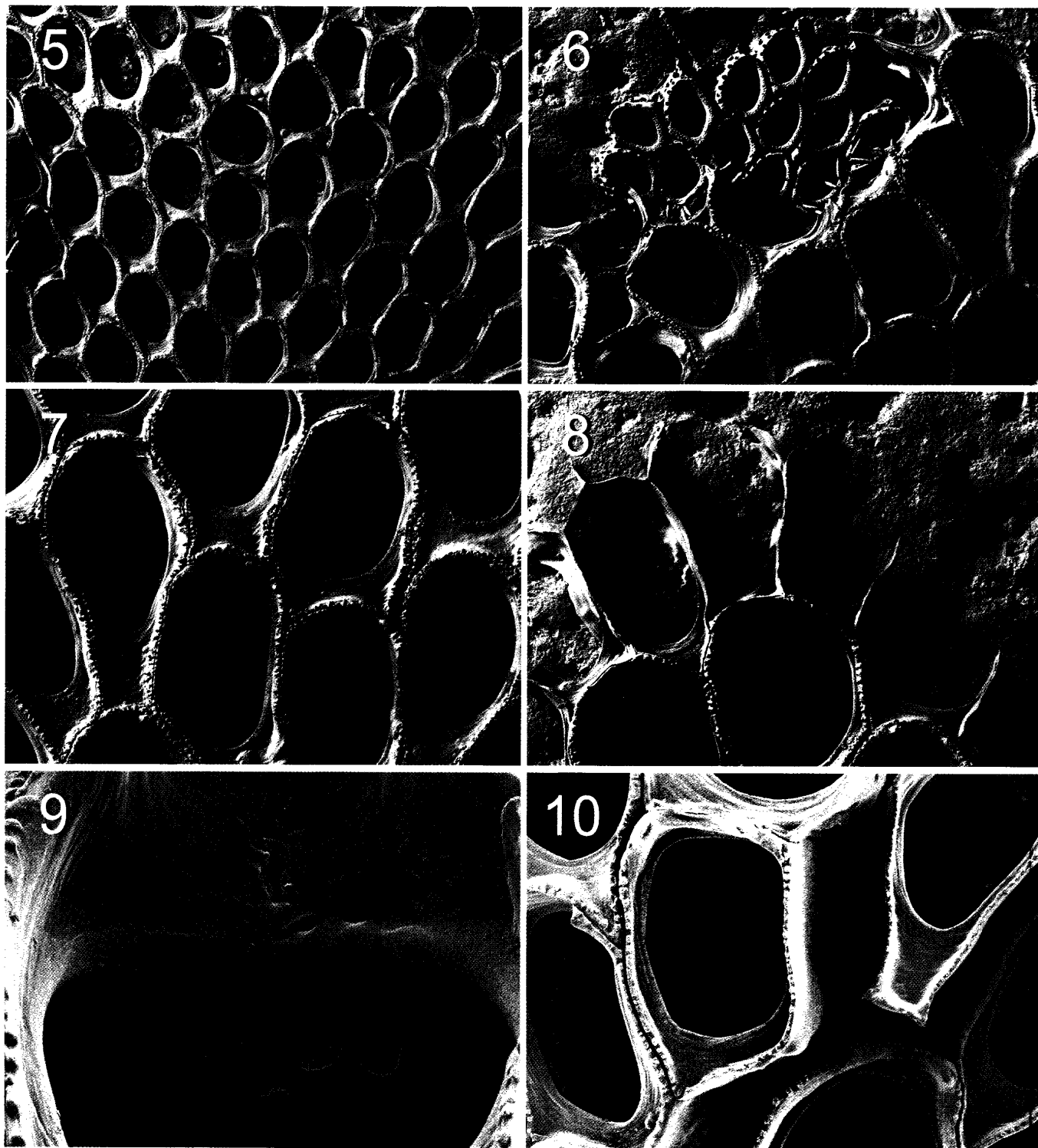
Description: Colony encrusting, multiserial (Figs 1, 5), unilamellar, rarely multilamellar, bright yellow in colour when alive, sallow or white when dry. Zooids extremely large (Figs 4, 6; Table 1), irregularly rhombic to oval, about 1.5 times longer than wide, approximately 500 µm deep, arranged more or less quincuncially; row bifurcations preceded by a wide zooid and followed by two narrow zooids, one of which is longer than the other (Fig. 2), re-establishing alternating arrangement of zooids. Zooidal boundaries in bleached specimens marked by fine sutures (Fig. 7), indicating position of cuticle between juxtaposed vertical exterior walls of adjacent zooids (Figs 15, 17, 18). Gymnocyst lacking. Cryp-



Figs. 1–4. *Gontarella gigantea* gen. et sp. nov. (1–3, ZIRAS 1/49944; 4, ZIHU-02049). 1. General view of the colony, $\times 5.3$. 2. Zooids from the central area of the colony showing yellow polypides and opercula with pale brown marginal thickenings, $\times 17.4$. 3. Colony margin showing developing zooids, $\times 10.9$. 4. General view of colony attached to a stone together with other bryozoan species and spirorbid worms, $\times 3.4$.

to cyst smooth, without granulation, depressed beneath level of zooidal boundary (Figs 7, 8), a narrow proximal shelf tapering distally, sometimes with a complete gap at distal extremity of zooid; irregular, convex, wart-like structures (Figs 5, 7) occasionally present on proximal cryptocyst. *Opesia* longitudinally oval in outline (Fig. 5), occupying most

of frontal area. Mural rim irregularly beaded. Pore chambers lacking. Vertical walls exterior (overbleached colonies split into single zooids); lateral vertical walls containing four, sometimes five, septulae with iris-like structure (Fig. 10); distal vertical walls containing numerous, rosette plates (Fig. 9), arranged in an irregular line, some uniporous, others



Figs. 5–10. *Gontarella gigantea* gen. et sp. nov. (5–8, NHM 2002.1.7.1; 9–10, ZIHU-02050), bleached. 5. Astogenetically mature zooids, $\times 11$. 6. Colony margin with zooids overgrowing *Cauloramphus spiniferum* (Johnston, 1832) illustrating the enormous size of the *G. gigantea* zooids, $\times 24$. 7. Detail of astogenetically mature zooids showing beaded mural rims and narrow cryptocysts, $\times 38$. 8. Growing edge of the colony showing developing zooids with thin lateral walls, partially calcified basal walls, and no pore chambers, $\times 37$. 9. Interior of the distal wall of a zooid, showing multiporous and uniporous septulae, $\times 200$. 10. Group of zooids becoming split through their independent vertical walls after overbleaching destroyed the intercalary cuticle, $\times 60$.

multiporous with up to four separate pores. Basal wall of zooids incompletely calcified (Fig. 8), an oval uncalcified window present. No ovicells, avicularia, or other polymorphs.

Frontal membrane translucent (Figs 1–3). Operculum semicircular, with pale brown marginal thickening (Fig. 2). Polypides yellow in alcohol-preserved specimen (Figs 1–3); tentacle number unknown.

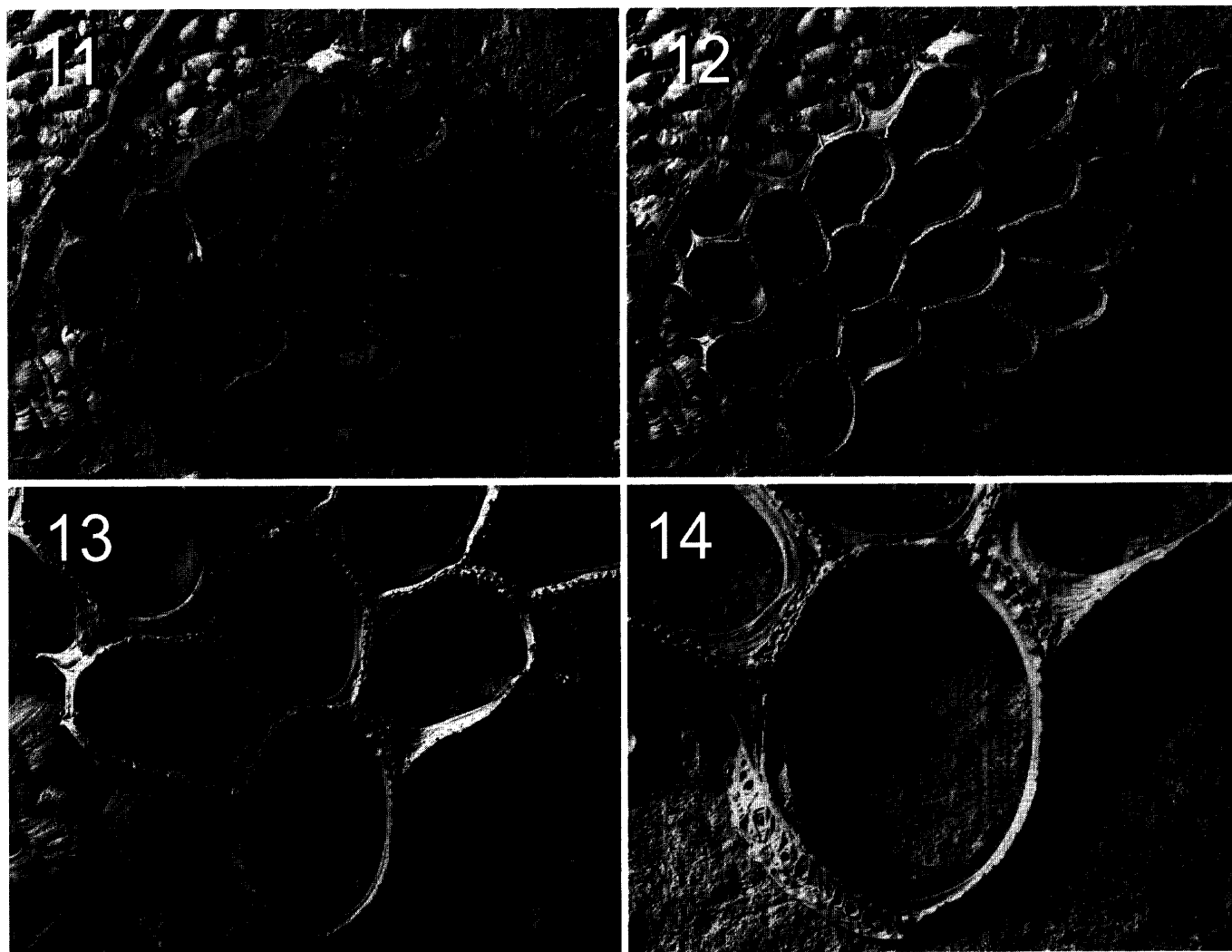
Ancestrula single, very large (Figs 11–14; Table 1), oval, lacking gymnocyst and with cryptocyst developed only as a very narrow proximal shelf, opesia occupying most of surface area. Mural rim beaded. Vertical walls concave, a narrow median septum at proximal extremity separating left and right sides of ancestrula; 7–8 pores present in each proximolateral vertical wall (Fig. 14). Basal wall containing uncalcified window. Ancestrula budding three zooids, one distal and two distolateral; additional zooids possibly budded laterally. Periancestrular zooids (Fig. 13) smaller than ancestrula, initiating a zone of astogenetic change with progressively increasing zooid size (Table 2).

Skeleton calcitic, moderately high in Mg, with estimated 8 per cent Mg substitution of Ca. Ultrastructural fabric finely

granular, some walls comprising wedge-shaped crystallites (Fig. 16) with fibrillar substructures. Ropey fabric (Fig. 18) visible at junction with cuticle in fractured compound vertical walls.

Remarks: *Gontarella gigantea* exhibits the simple skeletal morphology, including most notably a lack of ovicells and usually of avicularia, that is characteristic of the Malacostegia (see Taylor, 1987). Species belonging to this primitive, paraphyletic group of cheilostomes possess non-brooded cyphonautes larvae. Although the larva of *Gontarella* is yet unknown, it can be inferred that it is of this type. Malacostegians are generally classified into two families, Electridae and Membraniporidae. The Electridae as currently understood is a paraphyletic family that includes the oldest known cheilostomes. In contrast, the Membraniporidae are monophyletic and can be distinguished by the derived character of having a twinned ancestrula. The ancestrula of *G. gigantea* is single, excluding it from the Membraniporidae and placing the new genus and species in the Electridae.

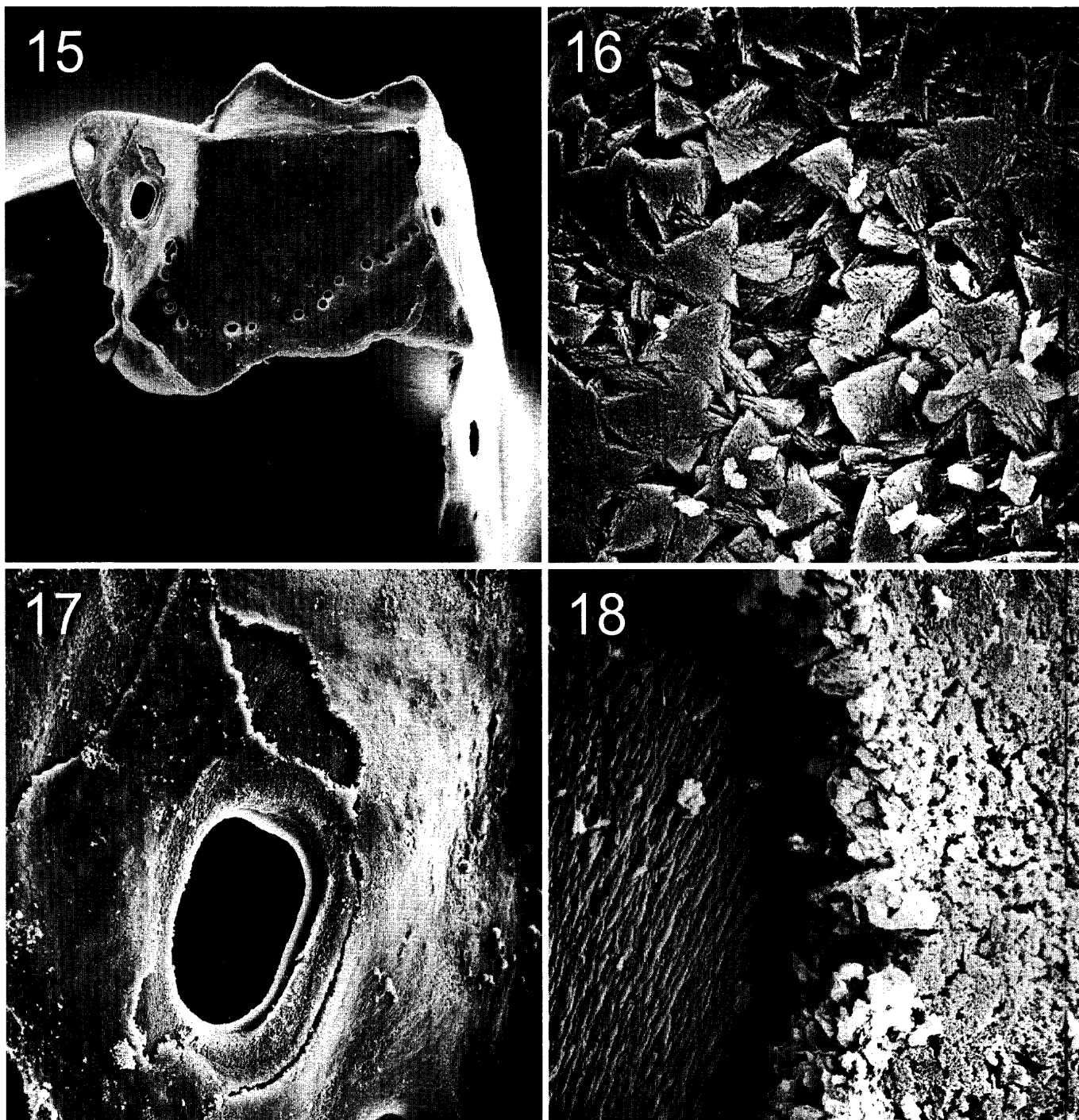
Three genera of Membraniporidae – *Membranipora* de Blainville, 1830, *Jellyella* Taylor and Monks, 1997, and



Figs. 11–14. *Gontarella gigantea* gen. et sp. nov., ancestrula and early astogeny (NHM 2002.1.7.2). 11. Small ancestrulate colony unbleached, $\times 15$. 12. Same colony after bleaching, $\times 16$. 13. Ancestrula with three periancestrular buds, $\times 38$. 14. Ancestrula with numerous septulae in proximolateral vertical walls, $\times 70$.

Acanthodesia Canu and Bassler, 1920 (often synonymised with *Biflustra* d'Orbigny, 1852 (Fig. 19) but, in the absence of data on the ancestrula in *Biflustra*, *Acanthodesia* is here retained) – have sheet-like encrusting colonies similar to *Gontarella*. All, however, can be distinguished from *Gontarella* by their twinned ancestrulae. In addition, the type species of *Membranipora* de Blainville, 1830, *M. membranacea* (Linnaeus, 1767) (Fig. 24), which is a specialized epiphyte, has: (1) lightly calcified rectangular zooids with tubercles at the corners; (2) a granulated but slight cryptocyst; (3) uncal-

cified bands in the lateral vertical walls; (4) multiporous septulae, two in each transverse wall, and four in each lateral wall; (5) 'tower' zooids; and (6) an aragonitic skeleton. The type species of *Jellyella* Taylor and Monks, 1997, *J. eburnea* (Hincks, 1891) (Fig. 20), has: (1) a moderately to well-developed gymnocyst produced into tubercles and/or spines proximally and around the opesium; (2) cryptocyst absent or forming a narrow, pustulose proximal shelf; (3) long spinules growing into the zooidal chamber; and (4) skeletal walls of calcite including a layer of spindle-shaped crystallites

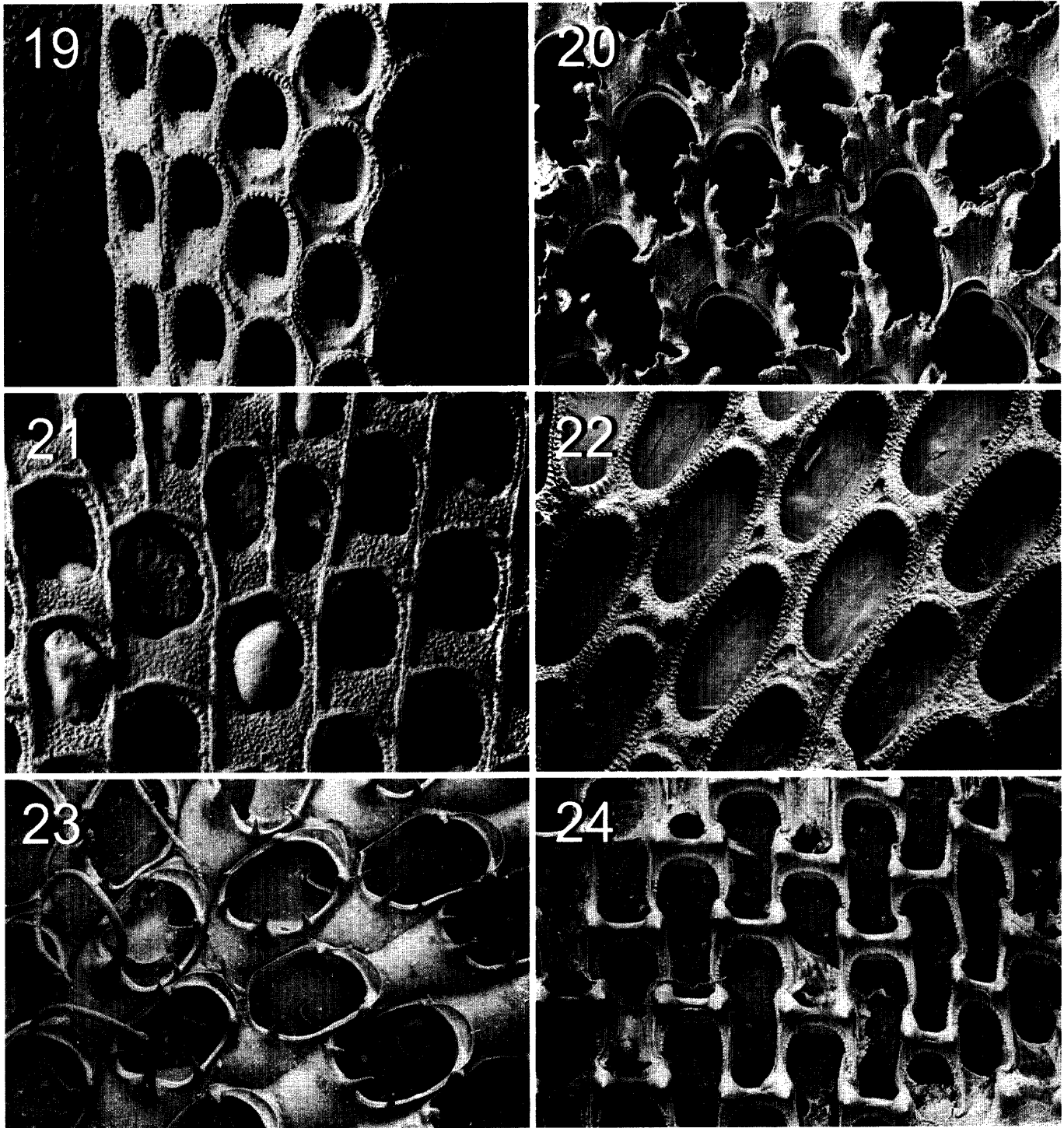


Figs. 15–18. *Gontarella gigantea* gen. et sp. nov., skeletal wall ultrastructure (ZIHU-02050). 15. Fragment viewed towards the distal wall of the zooid (contextual), $\times 110$. 16. Ultrastructure of wedge-shaped crystallites having fibrillar substructures visible on the surface of the distal wall, $\times 7000$. 17. Lateral wall with pore and window produced by partial exfoliation of the skeleton, $\times 600$. 18. Edge of exfoliation window showing vertical section through skeletal wall comprising fabric of wedge-shaped crystallites (right), and ropey texture (left) where wall of adjacent zooid is interpreted to have juxtaposed the intercalary cuticle, $\times 7000$.

arranged transversely to wall growth direction. The third membraniporid, *Acanthodesia* Canu and Bassler, 1920, the type species *A. savartii* (Audouin, 1826) (Fig. 21), has: (1) a well-developed, granulated, proximal; (2) no gymnocyst; (3) lateral walls with multiporous septulae; and (4) a lamellar calcitic skeleton.

Two common genera of extant electrids – *Conopeum* Gray, 1848, and *Electra* Lamouroux, 1816 – have sheet-like

encrusting colonies. Both can be distinguished from *Gontarella* in possessing pore chambers. In the type species of *Conopeum* Gray, 1848, *C. reticulum* (Linnaeus, 1767) (Fig. 22), additional differences from *Gontarella* include: (1) the gymnocyst and cryptocyst are narrow, the latter finely granular; (2) a variable number of small spines may sometimes be present, disposed regularly around the periphery of the zooid; (3) a pair of triangular chambers (kenozooids) are



Figs. 19–24. General views of colonies belonging to type species of some other malacostegan genera for comparison with *Gontarella*. 19. *Biflustra ramosa* d'Orbigny, 1852: Recent, Manilla, Philippines, MNHN, Paris, d'Orbigny Colln 13701, $\times 60$. 20. *Jellyella eburnea* (Hincks, 1891): Recent, Port Elizabeth, South Africa, NHM 89.1.1.1 (part), $\times 70$. 21. *Acanthodesia savartii* (Audouin, 1826): Recent, Alexandria, Egypt, NHM 1947.9.14.2, $\times 23$. 22. *Conopeum reticulum* (Linnaeus, 1767): Recent, Cheshire, UK, NHM 1961.5.8.1(a), $\times 59$. 23. *Electra pilosa* (Linnaeus, 1767): Recent, Calvados, France, NHM 99.7.1.1292, $\times 69$. 24. *Membranipora membranacea* (Linnaeus, 1767): Recent, Worthing Beach, Sussex, England, PDT Colln, January 1988, $\times 50$.

usually present at the distal angles of each zooid; and (4) the ancestrula buds two disto-lateral zooids, followed by a proximal zooid. The type species of *Electra* Lamouroux, 1816, *Electra pilosa* (Linnaeus, 1767) [= *E. verticillata* (Ellis and Solander, 1786)] (Fig. 23), has: (1) a moderately to well-developed gymnocyst containing apparent pores which are actually internal pits roofed by very thin calcification; (2) reduced, non-granular cryptocyst; (3) spines bordering the opesia, including a long median proximal spine. A third living electrid – *Aspidelectra* Levinsen, 1909 – is immediately distinguished from *Gontarella* by its costate frontal shield. Another electrid – *Villicharixa* Gordon, 1989 – has opesia ringed by articulated spines. Some additional electrid genera with sheet-like colonies are known only as fossils, including *Charixa* Lang, 1915, *Spinicharixa* Taylor, 1986, *Eokotosokum* Taylor and Cuffey, 1992, and *Bullaconopectum* Taylor, 1995. All are either spinose or have prominent gymnocystal tubercles, providing clear distinctions from *Gontarella*.

Ecology and Distribution. *Gontarella gigantea* is currently known from two widely-separated localities in the north-west Pacific: (1) the oceanic side of the Habomai Islands, Small Kuril Arc, (north-east of Hokkaido Island) and (2) the Western Kamchatka Shelf of the Sea of Okhotsk. Therefore, *G. gigantea* ranges at least between the latitudes of 43°10.2' and 67°37.0'N, and can be categorized as a Pacific Asiatic Wide-Boreal species.

G. gigantea has been recorded within areas of soft and mixed sea-bed (silt, sand, gravel) attached to hard substrata (stones, tubes of polychaetes and the hydrocoral *Allopora*

sp.). Known depth range is 78–535 m, with the more southerly occurrence being in deeper water.

DISCUSSION

The most remarkable feature of *Gontarella gigantea* is the enormous size of the zooids which average 1.55×0.97 mm in the holotype and can attain a length of 1.85 mm and width of 1.20 mm. To illustrate this we have compiled data from the literature (Kluge, 1975; Gostilovskaya, 1978; Ryland and Hayward, 1977; Winston, 1982; Gordon, 1984; Dick and Ross, 1988; Hayward, 1994, 1995; Hayward and Ryland, 1995; Soule *et al.*, 1995; Tilbrook, 1998; Winston *et al.*, 2000; Grischenko *et al.*, 2000; Tilbrook *et al.*, 2001) for a further 99 species of sheet-like encrusting anascan cheilostomes. These species were selected haphazardly from faunal studies describing bryozoans from different parts of the world. Values of mean or median (when range only was given) for zooid length and width were recorded as proxies for zooid size.

Expressed as the square root of length x width, the frequency plot of zooid size is strongly right-skewed (Fig. 25). Most species have small zooids, the modal value is closer to the minimum than maximum value, and a steadily declining number of species have large zooids. The long right tail of the distribution includes a gap between the second largest species and *G. gigantea* which has approximately twice the surface area. Therefore, for this data at least, *G. gigantea* forms a significant outlier of exceptional size.

Although beyond the scope of the present paper and

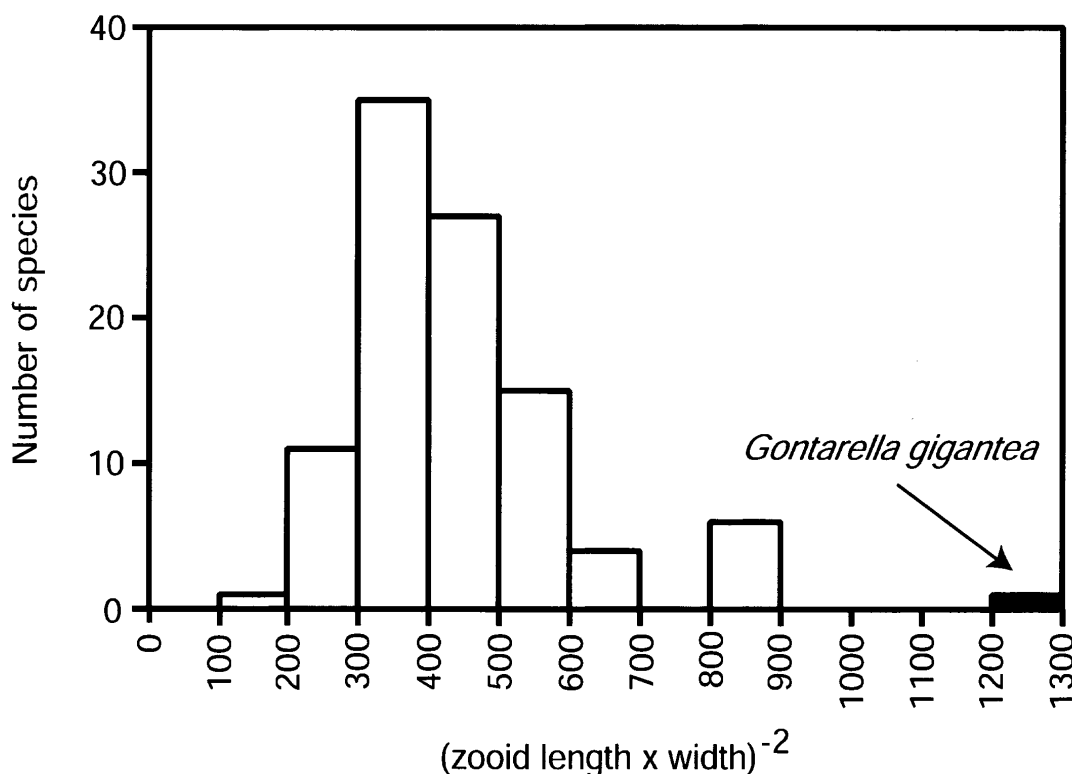


Fig. 25. Frequency distribution of zooidal size, expressed as the square root of length x width (in μm^2), in 100 species of anascan bryozoans with sheet-like encrusting colonies. Note the conspicuous outlier represented by *Gontarella gigantea* gen. et sp. nov.

warranting a much more detailed study, the form of the size frequency distribution deserves comment as we are unaware of any comparable analysis elsewhere for bryozoan zooid size. The pattern is very similar to that noted previously for body size in non-colonial organisms, as summarized by Brown (1995). In non-colonial groups as diverse as bacteria, trees, insects, fishes and mammals, Brown noted how there are: (1) many more species with small than large body sizes; and (2) that the distribution is highly right-skewed, with a sharp decline in number of species with progressively smaller body sizes from the mode, and a gradual decline in those with progressively larger body sizes.

In spite of the remarkably large zooid size of *G. gigantea*, it does not possess the largest zooids known for all fossil and extant cheilostome Bryozoa. The Cretaceous anascan *Herpetopora laxata* (d'Orbigny, 1852), with runner-like encrusting colonies has autozooids ranging up to 8.28 mm in length (Taylor, 1988). However, most of this length is taken up by a very narrow proximal part (cauda) whereas the 'functional' part of the autozooid containing the opesia is of normal dimensions. Autozooids of some recent cheilostomes with erect colonies can also attain a gigantic size. For instance, the erect Antarctic ascophoran *Antarcticaetos bubeccata* (Rogick, 1955) produces zooids 1.5–3.0 mm long by 0.5 mm wide (Hayward, 1995). Another Antarctic ascophoran with erect branching bilaminar colonies, *Cellarinellodes crassus* Moyano, 1970, has zooids 1.8–3.0 mm long by 0.5–0.6 mm wide (Hayward, 1995). Zooids in some Antarctic erect anascans are only a little smaller. Those of *Camptoplites rectilinearis* Hastings, 1943 are 2.3–2.5 mm long by 0.2 mm wide (Hayward, 1995), and *Klugeflustra antarctica* (Hastings, 1943) has zooids 1.5–2.5 mm long by 0.4 mm wide (Hayward, 1995).

Not only are the zooids from the zone of astogenetic repetition very large in *G. gigantea*, but the ancestrula is also gigantic. Table 3 lists ancestrular dimensions in some comparative anascan species with non-twinning ancestrulae. The linear dimensions of the *G. gigantea* ancestrula are almost twice the size of those of the next biggest species.

The larva of *Gontarella* is not yet known. However, on the basis of adult characters and the consequent systematic placement of the genus, the larva is inferred to be of the cyphonautes type, i.e. a bivalved, planktotrophic, non-brooded larva. In view of the large size of the ancestrula in *Gontarella* it is expected that the larva will also be large. The relationship between ancestrular size and the size of the mature cyphonautes larva for some malacostegan species shows that ancestrular length and larval maximum dimension are similar (Cook, 1962, 1964; Cook and Hayward, 1966). Therefore, the larva of *Gontarella* may be about 1 mm in maximum dimension, a size somewhat greater than the value of 850 µm for the largest cyphonautes (*Membranipora membranacea* (Linnaeus, 1767)) recorded in the British fauna (Ryland and Hayward, 1977) and which produces a twinned ancestrula on metamorphosis unlike the single ancestrula of *Gontarella*.

The physiological and ecological significance of large zooid size in *G. gigantea* is not understood. Observations of the limited material available suggest that *G. gigantea* is a good competitor for substrate space: colonies were frequently observed overgrowing other species of bryozoans but were never seen to be overgrown themselves. This matches the observations and predictions made by other authors. For bryozoans in general, competition for substrate space is aided by having large zooids, partly because large zooids have more powerful feeding currents potentially

Table 3. Comparison of ancestrula size in *Gontarella gigantea* gen. et sp. nov. with some other anascan membraniporiform cheilostome species having non-twinning ancestrulae.

Species	Ancestrula size, µm	Reference
<i>Gontarella gigantea</i> gen. et sp. nov.	1100×700	herein
<i>Smittipora abyssicola</i> (Smitt, 1873)	650×300	Ristedt, 1991: 379
<i>Calpensia nobilis</i> (Esper, 1796)	600×300	Ristedt, 1991: 373
<i>Antropora granulifera</i> (Hincks, 1880)	500×250	Ristedt, 1991: 372
<i>Amphiblestrum inermis</i> (Kluge, 1914)	400×400	Ristedt, 1991: 372
<i>Gregarinidra gregaria</i> (Heller, 1867)	400×300	Ristedt, 1991: 378
<i>Cranosina coronata</i> (Hincks, 1881)	400×240	Ristedt, 1991: 378
<i>Alderina imbellis</i> (Hincks, 1860)	380×300	Ryland and Hayward, 1977: 96
<i>Micropora brevissima</i> Waters, 1904	350×300	Ristedt, 1991: 379
<i>Andreella uncifera</i> (Busk, 1884)	350×300	Ristedt, 1991: 372
<i>Ellisina antarctica</i> Hastings, 1945	300×250	Ristedt, 1991: 378
<i>Callopora dumerilii</i> (Audouin, 1826)	300×240	Ristedt, 1991: 373
* <i>Electra monostachys</i> (Busk, 1854)	240×180	Ryland and Hayward, 1977: 70
* <i>Conopeum reticulum</i> (Linnaeus, 1767)	220×130	Ryland and Hayward, 1977: 60
* <i>Conopeum seurati</i> (Canu, 1928)	210×145	Ryland and Hayward, 1977: 62

* Indicates a malacostegan species known to have a cyphonautes larva.

capable of depleting food resources available to competitors (McKinney, 1993), and partly because the increased height of large zooids can present a greater physical obstacle to overgrowth by competitors (Buss, 1986).

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REFERENCES

- Audouin JV (1826) Explication sommaire des planches de polypes de l'Égypte et de la Syrie, publiées par Jules-César Savigny. *Descr Égypte Hist Nat* 1: 225–244
- Barnes DKA, Whittington M (1999) Biomechanics and mass mortality of erect bryozoans on a coral reef. *J Mar Biol Ass UK* 79: 745–747
- Blainville HMD de (1830) Zoophytes. In "Dictionnaire des Sciences naturelles, dans lequel on traite méthodiquement des différents êtres de la nature Vol 60" Ed by GF Cuvier, FG Levaillant, Paris, pp 1–546
- Brown JH (1995) Macroecology. Chicago University Press, Chicago
- Busk G (1852) An account of the Polyzoa, and sertularian zoophytes, collected in the voyage of the Rattlesnake, on the coasts of Australia and the Louisiade Archipelago. In "Narrative of the Voyage of HMS Rattlesnake" Ed by J MacGillivray, T and W. Boone, London, pp 343–402
- Buss LW (1986) Competition and community organization on hard surfaces in the sea. In "Community Ecology" Ed by J Diamond and TJ Case, Harper and Row, New York, pp 517–536
- Canu F, Bassler RS (1920) North American Early Tertiary Bryozoa. *Bull US Nat Mus* 106: 1–879
- Cocito S, Sgorbini S, Bianchi CN (1998) Aspects of the biology of the bryozoan *Pentapora fascialis* in the northwestern Mediterranean. *Mar Biol* 131: 73–82
- Cook PL (1962) The early larval development of *Membranipora seurati* (Canu) and *Electra crustulenta* (Pallas), Polyzoa. *Cah Biol Mar* 3: 57–60
- Cook PL (1964) The larval of *Electra monostachys* (Busk) and *Conopeum reticulum* (Linnaeus), Polyzoa, Anasca. *Cah Biol Mar* 5: 391–397
- Cook PL, Hayward PJ (1966) The development of *Conopeum seurati* (Canu), and some other species of membraniporine Polyzoa. *Cah Biol Mar* 7: 437–443
- Cook PL (1981) The potential of minute bryozoan colonies in the analysis of deep sea sediments. *Cah Biol Mar* 22: 89–106
- Dick MH, Ross JRP (1988) Intertidal Bryozoa (Cheilostomata) of the Kodiak vicinity, Alaska. Occasional Paper No 23, Center for Pacific Northwest Studies, Western Washington Univ, Bellingham, pp 1–133
- Ellis J, Solander D (1786) The natural history of many curious and uncommon zoophytes, collected... by the late John Ellis... systematically arranged and described by the late Daniel Solander.... Benjamin White and Son, London
- Gordon DP (1984) The Marine Fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge. *NZ Oceanogr Inst Mem* 91: 1–198
- Gordon DP (1989) New and little-known genera of cheilostome Bryozoa from the New Zealand region. *J Nat Hist* 23: 1319–1339
- Gostilovskaya MG (1978) Opredelitel Mshanok Belogo Morya. Nauka Press, Leningrad (in Russian)
- Gray JE (1848) List of the specimens of British animals in the collection of the British Museum. Part 1. Centroniae or Radiated Animals. Trust Brit Mus (Nat Hist), London, pp 91–151
- Grischenko AV, Gordon DP, Taylor PD (1999) A unique new genus of cheilostome bryozoan with reversed-polarity zooidal budding. *Asian Mar Biol* 15 (for 1998): 105–117
- Grischenko AV, Mawatari SF, Taylor PD (2000) Systematics and phylogeny of the cheilostome bryozoan *Doryporella*. *Zool Scr* 29: 247–264
- Hageman SJ, Bayer MM, Todd CD (1999) Partitioning phenotypic variation: genotypic, environmental and residual components from bryozoan skeletal morphology. *J Nat Hist* 33: 1713–1735
- Hastings AB (1943) Polyzoa (Bryozoa), – I. Scrupocellariidae, Epistomiidae, Farciminariidae, Bicellariellidae, Aeteidae, Scrupariidae. "Discovery" Rep 22: 301–510
- Hayward PJ (1994) New species and new records of Cheilostomatous Bryozoa from the Faroe Islands, collected by BIOFAR. *Sarsia* 79: 181–206
- Hayward PJ (1995) Antarctic Cheilostomatous Bryozoa. Oxford University Press, Oxford
- Hayward PJ, Ryland JS (1995) Bryozoa from Heron Island, Great Barrier Reef. 2. *Mem Queensland Mus* 38: 533–573
- Hincks T (1891) Contribution towards a general history of the marine Polyzoa. XV. South African and other Polyzoa. *Ann Mag Nat Hist* 6: 285–298
- Kluge GA (1975) Bryozoa of the northern seas of the USSR. Amerind Publishing Company Pvt. Ltd., New Delhi
- Lamouroux JVF (1816) Histoire des Polypiers Coralligènes Flexibles, vulgairement nommés Zoophytes. F Poisson, Caen
- Lang WD (1915) On some new uniseriate Cretaceous cheilostome Polyzoa. *Geol Mag* 6: 496–504
- Levinsen GMR (1902) Studies on Bryozoa. *Vidensk Medd Nat Foren Kjøbenhavn* 54: 1–31
- Levinsen GMR (1909) Morphological and systematic studies on the cheilostomatous Bryozoa. Nationale Forfatteres Forlag, Copenhagen
- Linnaeus C (1767) Systema Naturae. 12th edn. Vol. 1. Reginum Animale. Laurentii Salvii, Holmiae
- McKinney FK (1993) A faster paced world?: contrasts in biovolume and life-process rates in cyclostome (Class Stenolaemata) and cheilostome (Class Gymnolaemata) bryozoans. *Paleobiology* 19: 335–351
- McKinney FK, Jackson JBC (1989) Bryozoan Evolution. Unwin Hyman, Boston
- Moyano GHI (1970) Bryozoa colectados por la Expedicion Antartica Chilena 1964–65. IV. Familia Arachnopusiidae Jullien, 1888. *Bol Soc Biol Concepción* 42: 257–285
- O'Dea A, Okamura B (1999) Influence of seasonal variation in temperature, salinity and food availability on module size and colony growth of the estuarine bryozoan *Conopeum seurati*. *Mar Biol* 135: 581–588
- Orbigny AD d' (1851-4) Paléontologie française. Descriptions des Mollusques et rayonnés fossiles. Terrains crétacés, V. Bryozoaires. Victor Masson, Paris
- Ristedt H (1991) Ancestrula and early astogeny of some anascan Bryozoa; their taxonomic importance and possible phylogenetic implications. In "Bryozoaires Actuels et Fossiles: Bryozoa Living and Fossil" Ed by FP Bigey and J-L d'Hondt, *Bull Soc Sci Nat l'Ouest France, Mém HS* 1, pp 371–382
- Rogick MD (1955) Genus *Emballothea* Levinsen 1909. *Trans Amer Microscop Soc* 74: 103–112
- Ryland JS (1975) Parameters of lophophore in relation to population structure in a bryozoan community. In "Proceedings of the 9th European Marine Biology Symposium" Ed by H Barnes, Aberdeen Univ Press, pp 363–393
- Ryland JS, Hayward PJ (1977) British anascan bryozoans. *Synopses of the British Fauna (New Ser)* 10: 1–188

- Soule DF, Soule JD, Chaney HW (1995) The Bryozoa. In "Taxonomic Atlas of the Santa Maria Basin and Western Santa Barbara Channel Vol 13" Eds by JA Blake, HW Chaney, PH Scott and AL Lissner, Santa Barbara Mus Nat Hist, Los Angeles, pp 1–344
- Stach LW (1937) Reports of the McCoy Society for Field Investigation and Research. Lady Julia Percy Island. 13. Bryozoa. Proc Royal Soc Victoria (New Ser) 49: 373–384
- Taylor PD (1986) *Charixa* Lang and *Spinicharixa* gen. nov., cheilostome bryozoans from the Lower Cretaceous. Bull Brit Mus (Nat Hist) (Geol Ser) 40: 197–222
- Taylor PD (1987) Skeletal morphology of malacostegan grade cheilostome Bryozoa. In "Bryozoa: present and past" Ed by JRP Ross, Western Washington Univ, Bellingham, pp 269–276
- Taylor PD (1988) Colony growth pattern and astogenetic gradients in the cretaceous cheilostome bryozoan *Herpetopora*. Palaeontology 31: 519–549
- Taylor PD (1995) Late Campanian-Maastrichtian Bryozoa from the United Arab Emirates-Oman border region. Bull Nat Hist Mus (Geol Ser) 51: 267–273
- Taylor PD, Cuffey RJ (1992) Cheilostome bryozoans from the Upper Cretaceous of the Drumheller area, Alberta, Canada. Bull Brit Mus (Nat Hist) (Geol Ser) 48: 13–24
- Taylor PD, Monks N (1997) A new cheilostome bryozoan genus pseudoplanktonic on molluscs and algae. Invert Biol 116: 39–51
- Tilbrook KJ (1998) The species of *Antropora* Norman, 1903 (Bryozoa: Cheilostomatida), with description of a new genus in the Calloporoidea. Rec South Austral Mus 31: 25–49
- Tilbrook KJ, Hayward PJ, Gordon DP (2001) Cheilostomatous Bryozoa from Vanuatu. Zool J Linn Soc 131: 35–109
- Winston JE (1982) Marine bryozoans (Ectoprocta) of the Indian River area (Florida). Bull Amer Mus Nat Hist 173: 99–176
- Winston JE, Hayward PJ, Craig SF (2000) Marine bryozoans of the northeast coast of the United States: new and problem species. In "Proceedings of the 11th International Bryozoology Association Conference" Ed by A Herrera Cubilla and JBC Jackson, Balboa, Republic of Panama: Smithsonian Trop Res Inst, pp 412–420

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